

a. Green and colleagues 1963

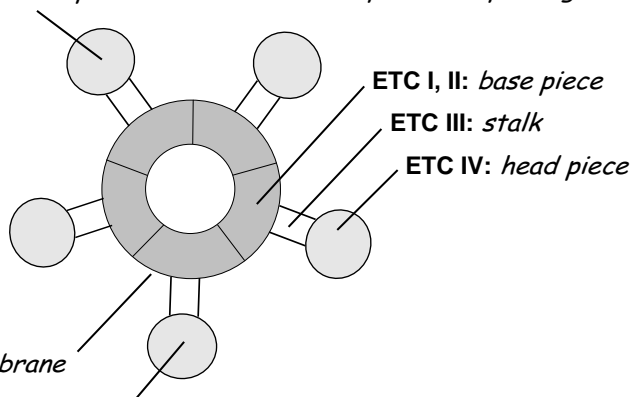
ETC: *inner membrane sphere*

b. Green and colleagues 1964

ETC: *tripartite repeating unit*

c. Racker 1965

ETC: *inner membrane*



Oxidative phosphorylation (ATPase): *inner membrane sphere*

Figure 6.7. Three proposals as to the significance of the spherical particles on the mitochondrial inner membrane (cristae). (a) Green's 1963 proposal, in which each inner membrane sphere contained an entire electron transport chain (ETC). (b) Green's revised proposal of a tripartite repeating unit in which complexes I and II of the electron transport chain were contained in the base piece, complex III in the stalk, and complex IV in the head piece. (c) Racker's account localizing ATPase in the inner membrane spheres and the electron transport chain in the inner membrane.

cristae into the inner mitochondrial milieu. While small, these particles are numerous, with estimates of 10,000 to 100,000 per mitochondrion. When he applied the negative stains without prior fixation, mitochondria swelled and burst, extruding membranous material in the form of sheets, tubules, or ribbons that were studded with small spherical knobs about 90 Å in diameter. These spherical knobs can readily be seen (particularly in the inset) in Figure 6.6, which shows a micrograph Fernández-Morán published in 1964.

Green seized upon Fernández-Morán's discovery, naming the knobs *inner membrane spheres* and proposing that they constituted the complete system of enzymes for electron transport (Figure 6.7a). Lehninger (1964), however, calculated that the weight of the respiratory assembly was one to two orders of magnitude greater than that of these particles. As shown in Figure 6.7b, Green and his collaborators then proposed a distribution of the four different complexes of enzymes involved in electron transport over the base piece (Complexes I and II), stalk (Complex III), and head piece (Complex IV), respectively (Fernández-Morán et al., 1964). Although much of their analysis focused on the relative sizes of the stalk and head pieces and the minimum